An Extended Food Web from Greenland

Adding birds, spiders and plants to a parasitoid-lepidopteran web

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Master's Thesis
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Tiivistelmä – Referat – Abstract

Quantitative food webs have been used since the 1990s to describe the ecology of ecosystems. Such webs describe not only 'who eats whom' but also how many individuals get eaten, giving a detailed picture of the connections in an ecosystem. This detail allows far-reaching ecological conclusions to be drawn, for all manner of questions ranging from the influence of abiotic and biotic factors on population dynamics to the effect of latitude on ecosystem structure. Currently the webs' greatest limitations are their incompleteness and lack of geographic coverage: most published webs focus on a tiny fragment of the total food web, and there are few webs from higher latitudes. In this thesis I address these limitations, by extending a parasitoid-lepidopteran web which is being collected in the High Arctic. I add data on bird and spider predation of the web's Lepidoptera, and on the lepidopterans' herbivory of their food plants. Specifically, I ask what the relative strengths of predation and parasitism are in this community, and what effect herbivory has on the plants' seed production.

I measured predation rates using both live caterpillars and modelling clay dummies as bait. The former, caterpillars of *Sympistis nigrita* tethered to threads, gave an estimate of both spider and bird predation. The latter showed bird predation only, but gave a larger sample size than tethered caterpillars. For the herbivory rates, I measured the seed production of avens flowers (*Dryas octopetala x integrifolia*, one of the main lepidopteran food plants) when damaged by feeding caterpillars.

I found that predation is an important cause of mortality for *S. nigrita*, comparable to the high rates of parasitism already observed. During the larval period, some 38% of *S. nigrita* caterpillars are killed by spiders, 8% by parasitoids and 8% by birds. The caterpillars ate highly variable amounts of avens flowers, with 14.4% of flowers damaged by feeding in a set of 743 flowers, and 8.3% in another set of 672 flowers. The damaged flowers produced fewer and smaller seeds than did undamaged ones, causing overall avens seed production to drop by 7%.

Overall, my findings show spider predation to be a relevant addition to the current parasitoid-lepidopteran food web. Bird predation, however, is relatively light – both when compared to spider predation and also to earlier predation rates reported from warmer latitudes. It is nevertheless comparable to the (naively twice as strong) parasitism since almost half the parasites die when their host is predated. When comparing food webs in order to address large scale ecological questions, such as the effect of latitude on food web structure, broader webs may be required instead of the mere parasitoid-host webs produced to date.

Avainsanat – Nyckelord – Keywords quantitative food webs, Zackenberg, predation, parasitism, tethered larvae, dummy larvae, *Dryas octopetala x integrifolia*, *Sympistis nigrita*

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Tiivistelmä – Referat – Abstract

Määrällisiä ravintoverkkoja on käytetty 1990-luvulta lähtien kuvaamaan ekosysteemien ekologiaa. Niistä selviää sekä kuka syö ketäkin että kuinka moni yksilö tulee syödyksi – antaen tarkan kuvan lajien välisistä vuorovaikutuksista. Tällainen yksityiskohtainen ekosysteemin kuvaus mahdollistaa lukuisten ekologisten kysymysten käsittelemisen, aina abioottisten ja bioottisten tekijöiden vaikutuksesta populaatioihin siihen, miten eliöyhteisojen rakenne vaihtelee leveyspiirin mukaan. Nykyisellään ravintoverkkojen suurimpana heikkoutena on kattavuuden puute: useimmat julkaistut verkot sisältävät vain murto-osan alueen lajeista, eikä verkkoja juurikaan ole kuvattu kylmiltä leveyspiireiltä. Työssäni täydennän verkkoja kattavammiksi laajentamalla loisten ja perhosentoukkien verkkoa, jota kerätään parhaillaan Grönlannissa: lisään verkkoon perhosentoukkien saalistajat (linnut ja hämähäkit) sekä toukkien ravintokasvin.

Selvitin saalistuksen määrän levittämällä maastoon syötteinä sekä eläviä perhosentoukkia että muovailuvahasta tehtyjä keinotoukkia. Elävien toukkien – eli lankaan kiinnitettyjen *Sympistis nigrita* -toukkien – avulla selvitin lintujen ja hämähäkkien saalistamien toukkien määrän. Keinotoukat mittasivat ainoastaan lintujen saalistusta, mutta suuremmalla otoksella. Kasvinsyönnin laajuutta arvioin toukkien yleisimmästä ravintokasvista lapinvuokosta (*Dryas octopetala x integrifolia)*. Mittasin kuinka moni kukista joutui toukkien syömäksi ja miten tämä vaikutti siementuottoon.

Saalistus osoittautui merkittäväksi *S. nigrita* -toukkien kuolinsyyksi ja oli mitattua loisintaa voimakkaampaa. Kaiken kaikkiaan 38% toukista joutuu hämähäkin, 8% loisen ja 8% linnun syömäksi. Toukat söivät lapinvuokkoa vaihtelevissa määrin: 743 kukan otoksesta toukat olivat vahingoittaneet 14.4%, ja 672 kukan otoksesta 8.3% oli vahingoittunut. Vahingoittuneet kukat tuottivat vähemmän ja pienempiä siemeniä, minkä seurauksena lapinvuokon siementuotto väheni 7%.

Tulosteni perusteella hämähäkit ovat Grönlannissa merkittäviä perhosentoukkien saalistajia ja ne kuuluu lisätä nykyiseen loisten ja perhosentoukkien verkkoon. Linnut sen sijaan saalistavat verraten vähän toukkia – sekä hämähäkkeihin verrattuna että myös siihen verrattuna, mitä lintujen on raportoitu saalistavan eteläisemmillä leveyspiireillä. Lintujen suorittama saalistus on kuitenkin verrattavissa loisintaan (15%), koska monet loiset kuolevat isäntänsä mukana saalistukseen jolloin lopullinen loisintaosuus puolittuu. Tulevaisuudessa saatetaan tarvita nykyisiä lois-isäntä -verkkoja laajempia ravintoverkkoja, jos ekologisia kysymyksiä halutaan ratkoa vertaamalla eri alueiden ravintoverkkoja. Näin voitaisiin esimerkiksi selvittää leveyspiirin vaikutusta eliöyhteisön rakenteeseen.

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1. Introduction

Almost by definition, an ecologist studies interactions: both biotic interactions between living organisms, and abiotic interactions between organisms and their physical environment. Most items of interest, such as population dynamics and abundances, can in principle be deduced from these. Since the strongest interactions involve the death of an individual, and feeding is often the cause of that death, food webs are an obvious way to describe the ecology of ecosystems.

Classically, food webs represent species as linked to each other according to who eats whom. Such visually appealing webs have been in use since at least the early 20th century (Egerton 2007). They are relatively easy to acquire and can be quite descriptive. (For example, species can at a glance be divided into guilds of herbivores, predators etc.) However, they contain little or no information on the strength of an interaction. This makes it difficult to draw far-reaching ecological conclusions from them: important links are treated on a par with rare ones, and a combination of chance and sampling effort largely dictates which rare links are included in a web (Goldwasser & Roughgarden 1997, Martinez et al. 1999, Van Veen et al. 2006).

Many of a classical web's disadvantages can be alleviated by quantifying its links. Instead of merely noting who eats whom, a quantitative web shows how many individuals are eaten – giving detailed knowledge of the relative size of the links (Memmot et al. 1994, Van Veen et al. 2006, Banašek-Richter et al. 2009). Quantitative food webs are laborious to construct, so all published webs have been restricted to a subset of the total web – typically describing invertebrate communities (such as parasitoids and their hosts) in temperate (e.g. Müller et al. 1999, Rott & Godfray 2000, Valladares et al. 2001) or tropical regions (e.g. Memmot et al. 1994, Lewis et al. 2002). In practice this restriction is often unavoidable, but may lead to important parts of a web being missed: a web consisting of hosts and their parasitoids is incomplete if the hosts are also eaten by birds. Indeed, there are known cases of bird predation being comparable to parasitism (Brown et al. 1995) and at least one gall midge–parasitoid web appears to be structured by bird

predation (Tscharntke 1992). In real life, most species in an area are likely linked to each other to some extent (Pocock et al. 2012).

How different factors (both biotic and abiotic) affect a food web and its species has long been debated. On the biotic side, a long-standing question was whether populations are primarily regulated by predators (top-down) or by their food source (bottom-up) (Hairston et al. 1960, Murdoch 1966, White 1978, Power 1992). This discussion has now largely undergone a synthesis, where the relative importance of top-down vs. bottom-up is thought to vary between different locations and times (Hunter & Price 1992, Gripenberg & Roslin 2007). The relative role of competition between species (Denno et al. 1995, Kaplan & Denno 2007) and of abiotic factors (e.g. Kitching 2000, Oksanen & Oksanen 2000) has also been inconclusively debated.

In this context, a still open question is how different sources of mortality, and consequently food web structure, vary with latitude. At high latitudes primary productivity is generally low and abiotic conditions harsh. This translates into ecosystems with few species, and has been predicted to cause simple food webs with few trophic levels (Pimm 1982, Kitching 2000) that are dominated by abiotic factors (Van der Wal & Hessen 2009, also Oksanen & Oksanen 2000 for vertebrate food webs). However, in the absence of quantitative food webs from high latitudes, such theoretical ideas on the effect of latitude are doomed to remain theoretical.

In this thesis, I contribute to the ongoing construction of the first quantitative food web from the High Arctic. Since 2009 data has been gathered on a web of Lepidoptera and their parasitoids at Zackenberg valley, NE Greenland. While detailed, this web is incomplete since it ignores the interactions between Lepidoptera and plants, and also interactions with predators such as birds. I extend the current parasitoid-lepidopteran web to cover interactions at three trophic levels by asking the following questions:

1) How do the Lepidoptera affect their food plants? Or specifically: What fraction of flowers are eaten by caterpillars, and how does this affect seed production?

2) How do predators (other than the parasitoids) affect the Lepidoptera? Or specifically: How large are predation rates by birds and spiders compared to parasitism rates?

By answering these questions, I contribute to the quest for a *complete*, *quantitative* food web from this high latitude.

2. Materials & Methods

To broaden the existing parasitoid-lepidopteran food web to cover three trophic levels, I measured three types of interactions: ***1)*** For the plant-herbivore link in the food web, I chose an important lepidopteran food plant, avens (*Dryas octopetala x integrifolia*). I examined avens flowers for damage caused by feeding caterpillars, and measured the subsequent drop in the flowers' seed production. ***2)*** For quantifying the herbivore-predator link, I examined rates of attack on (mainly) *S. nigrita* caterpillars. I divided these into attacks caused by spiders and birds. ***3)*** Finally, to bring together the different parts of the food web, I quantified the herbivore-parasitoid link based on known parasitism data, and calculated the relative strength of the food web's interactions.

2.1. Study system (Zackenberg, NE Greenland)

Zackenberg research station (74°30'N / 21°00'W) is located in the Zackenberg valley of Northeastern Greenland, by the coast on the narrow band of terrestrial life between the Arctic sea and the inland ice sheet. Apart from some fur trapping in the first half of the 20th century and some Inuit inhabitants in earlier centuries, the area has been virtually untouched by humanity (see e.g. Meltofte et al. 2008).

The valley is characterised by short tundra vegetation, with plants such as avens (*Dryas octopetala x integrifolia*), arctic willow (*Salix arctica*) and *Cassiope tetragona* dominating much of the landscape (for more detail on the vegetation, see Bay 1998). The

plants are fed on by lepidopteran caterpillars, which in turn are preyed on by parasite wasps, birds and (as it turned out during this study) spiders (Fig. 1).

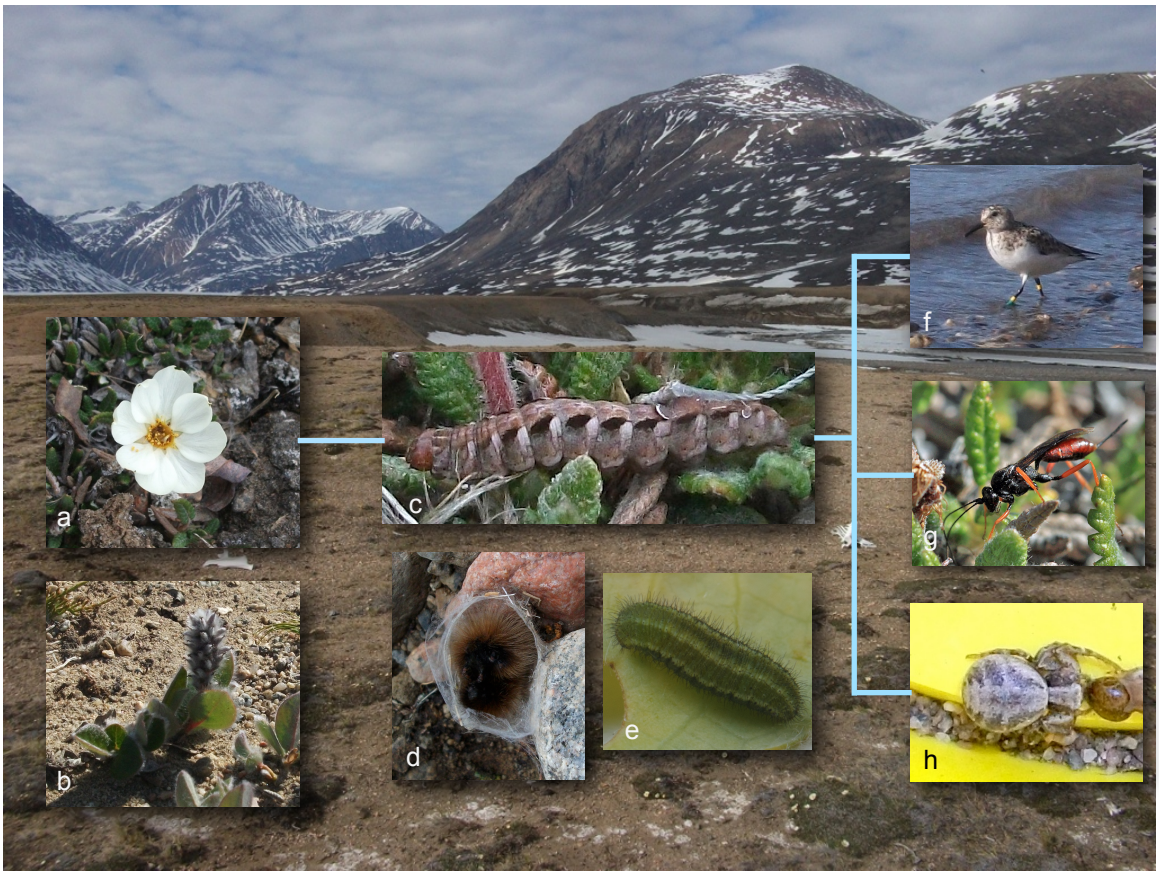

Fig. 1. The study system in a nutshell: plants, herbivores and their predators at Zackenberg. **Left:** The two most important lepidopteran food plants **a)** Avens *Dryas octopetala x integrifolia* **b)** Arctic willow *Salix arctica.* **Centre:** Three of the valley's nineteen lepidopteran species **c)** *Sympistis nigrita* **d)** *Gynaephora groenlandica* **e)** *Colias hecla* **Right:** Main predators of the Lepidoptera. **f)** Birds (e.g. Sanderling *Calidris alba* ♂) **g)** Parasitoids (e.g. *Cryptus arcticus* ♀, photo courtesy of Gergely Várkonyi) **h)** Spiders (e.g. crab spiders in family Thomisidae). The lines show the main focus of this study, tritrophic interactions between avens (a), *S. nigrita* (c) and its predators (f,g,h). I also investigated bird predation on the two other lepidopterans (d,e).

Of the nineteen known lepidopteran species in the Zackenberg valley (Roslin & Várkonyi unpublished data: for a preliminary overview see Roslin & Várkonyi 2010), I focused mainly on the locally most common species *Sympistis nigrita* (Fig. 1c). The species has a two year life cycle, hatching from eggs in early spring, pupating after 3–4 weeks in July–August, then hatching as an adult the next summer. Caterpillars are to be found in large numbers wherever their sole food plant avens (Fig. 1a) is flowering. Early instars eat only the flowers, concentrating on the pistils and stamens. Later in the season, once the flowers start wilting, the older instars shift their diet to the leaves. Almost all feeding damage to

avens seems to be caused by *S. nigrita*, presumably because it so outnumbers the other avens eaters.

Apart from *S. nigrita*, I also measured bird predation rates on caterpillars of *Gynaephora groenlandica* (Arctic woolly bear, Fig. 1d) and *Colias hecla* (Northern clouded yellow, Fig. 1e). *G. groenlandica* are common throughout the Zackenberg valley, eating arctic willow (*Salix arctica,* Fig. 1b). They have an exceptionally long life cycle, presumed to stretch over seven years (Morewood & Ring 1998). The caterpillars are active for only a few weeks from mid June to mid July, and pass but one instar each year. Little is known about the *C. hecla* of Greenland, though the adults are a common sight. As I found two caterpillars in the fen-like vegetation (i.e. moss, arctic willow, *Eriophorum*) by streams, I assumed this to be their typical habitat at Zackenberg. Their food plant appears to be arctic willow and the young caterpillars are active in (at least) August, hibernating as early instars.

The valley hosts several potential predators and parasites of the Lepidoptera. The food web of parasitoid wasps, tachinids and Lepidoptera has been studied since 2009, with 27 known parasitoid species at the time of writing in families Hymenoptera: Ichneumonidae, Hymenoptera: Braconidae and Diptera: Tachinidae (Roslin & Várkonyi unpublished data: for a preview see Roslin & Várkonyi 2010; Fig. 1g). Likely lepidopteran-eating birds include numerous sandpipers (e.g. sanderling *Calidris alba,* Fig. 1f), snow buntings *Plectrophenax nivalis* and long-tailed skuas *Stercorarius longicaudus* (Table 1). Crab spiders in the family Thomisidae and wolf spiders in Lycosidae are the main invertebrate predators (Fig. 1h), with no ants and virtually no predatory beetles to be found in the area.

Table 1. Bird abundance at the study site, based on the 2011 monitoring at Zackenberg (courtesy of Jannik Hansen). Shown as the number of nesting territories in a 7.77 km^2 area, less than 50 m above sea level (see map in Appendix 1). Comparable estimates are not yet available for spiders, parasitoids, or other members of the food web.

Bird species	**Territories / 7.77 km^2**
Common ringed plover *Charadrius hiaticula*	8
Red knot *Calidris canutus*	9–13
Sanderling *Calidris alba*	32–33
Dunlin *Calidris alpina*	74–80
Ruddy turnstone *Arenaria interpres*	18–23
Long-tailed skua *Stercorarius longicaudus*	8–10
Arctic redpoll *Carduelis hornemanni*	1–2
Snow bunting *Plectrophenax nivalis*	38

2.2. Measuring plant-herbivore interactions

To quantify the link between plants and herbivores, I measured the portion of avens flowers that had been eaten by caterpillars. I also measured the seed production of such flowers, since this gives a direct estimate of the caterpillars' effect on avens fitness.

In order to measure the portion of avens flowers eaten by caterpillars, I inspected the flowers in 22 square plots of 1 metre x 1 metre (referred to as 'square plots'). I selected the plots haphazardly on the 21st June 2011 by throwing a hat in the air, then finding the nearest flowering avens to where it landed (for a map, see Appendix 1). As additional material, I also checked the flowers within a 20 cm radius of 65 dummy *S. nigrita* used as bait ('other plots'; see below under 2.2.2). I classified all the flowers in a plot or around a dummy into four categories: 1) *undamaged* 2) *pistil eaten* 3) *stamens eaten* 4) *all eaten* (Fig. 2). I ignored damage to petals since the caterpillars barely touched them.

Fig. 2. Avens flowers that have been eaten by caterpillars. I classified flower damage into four categories: **a)** *Undamaged* **b)** *Stamens:* The stamens are (partly or wholly) missing, but the pistil is intact. **c)** *Pistil:* The pistil is at least partly eaten. Some stamens may also be missing. **d)** *All:* Both pistil and stamens have been eaten.

In order to measure the seed production of damaged flowers, I marked 17 flowers of each category (68 in all) with red crepe tied round the stalk. These marked flowers were all in the square plots, with no plot containing more than three flowers of a category. Once the avens had finished flowering on the 19th July 2011 I collected the seeds, and counted and weighed them after drying. In practice (since the seeds were often too numerous to count) I weighed and counted 15 or more of a flower's seeds, then estimated the total number of seeds from their weight (Fig. 3).

Fig. 3. Weighing and counting an avens flower's seeds. I counted a subset of 15 or more of a flower's seeds which I weighed with the fluff attached, then weighed all the seeds (with fluff attached). This gave an estimate of the total number of seeds. I also weighed the subset of seeds with fluff removed, giving an estimate of the average seed weight.

2.2.1. Analyses of plant-herbivore interactions

To estimate the average percentage of flowers damaged by caterpillars and its variation I used bootstrapping (see Efron & Tibshirani 1993). Briefly, I set a computer to randomly resample the plots with replacement 10^6 times, and took the average and standard deviation of the ensuing 10^6 flower damage percentages. Less briefly, using the 22 square plots as an example: 1) a new sample of 22 plots was drawn randomly from the original square plots (with replacement, i.e. the same plot could be drawn several times) 2) the average flower damage was calculated for this new sample 3) the previous two steps were repeated 10^6 times giving a distribution of 10^6 flower damage percentages. I took the mean and standard deviation of this (more or less normal) distribution, which correspond to the average flower damage at the study site and its standard error. I calculated the bootstraps using the R software (version 2.9.0).

Following Agrawal (1998), I estimated the herbivory's effect on avens fitness by calculating the total weight of seed produced by a flower (i.e. seed weight *x* amount of seeds). I used a Kruskal-Wallis test to compare the relative fitness of the four categories of flower damage, and used the same test for comparing the amount of seeds produced and the average seed weight. The data was not normally distributed, so the Kruskal-Wallis test was better suited for comparing the damage categories than an ANOVA.

2.3. Measuring herbivore-predator interactions

To measure the rate at which caterpillars were attacked by predators, I used a combination of two methods: first, I tethered live *S. nigrita* to threads, and second, I placed dummy *S. nigrita* on avens flowers (for an overview of when the baits were in use, see figure 4). Both approaches involved exposing the caterpillars (either real or artificial) as bait and checking them later for signs of attack.

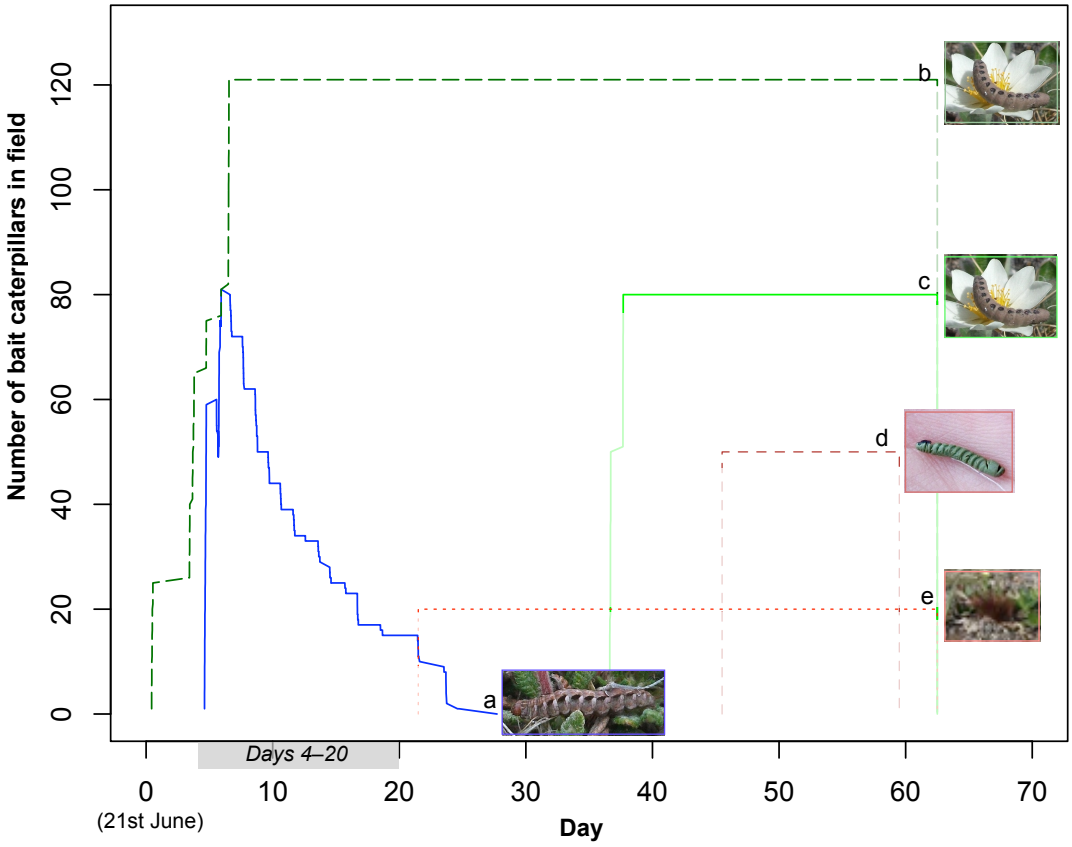

Fig. 4. Time of exposure for different types of bait. The main data on predation derived from **a)** tethered *S. nigrita* and **b)** dummy *S. nigrita*. A second group of dummy *S. nigrita* (**c**), and some dummy *C. hecla* (**d**) and *G. groenlandica* (**e**) were exposed for a shorter time. I removed most dummy baits on day 62, the 22nd August. In the analyses, I compared tethered *S. nigrita* (a) to dummies (b) based on attack rates during days 4–20, when both were in use simultaneously.

The first method used real live *S. nigrita* as bait, giving a realistic estimate of both spider and bird predation rates. As this method required live caterpillars, which were only available early in the season and were time-consuming to collect, I used dummy *S. nigrita* as a second method (see e.g. Howe et al. 2009). The latter gave an estimate of bird (but not spider) attack rates for the whole season. Importantly, I compared the two methods'

results for the early season (when both were in use simultaneously, Fig. 4): dummies do not move so their likelihood of being attacked could have been different to that of live caterpillars.

To check whether the predation rates on *S. nigrita* are comparable to those on other species, I also placed dummy *G. groenlandica* and *C. hecla* in the field.

2.3.1. Tethered *S. nigrita*

To measure spider predation rates, and as one of two methods for measuring bird predation rates, I tethered 81 live *S. nigrita* in groups of five (Fig. 6; one group had an extra *S. nigrita*). I spaced the groups out haphazardly, trying to cover as wide a range as possible (see map in Appendix 1: Fig A1.3). The *S. nigrita* were locally collected on the 20th June and reared for 5–6 days until they had reached their last or next to last instar. At first I tethered them using fishing line (42 caterpillars on lengths of line). However, this line proved too stiff and many caterpillars died when unable to shelter under avens leaves. I therefore switched to using polyester sewing thread for the remainder (63 caterpillars tethered to thread, partly replacing dead individuals). 24 caterpillars died soon after tethering (all but one on fishing line) and had to be replaced.

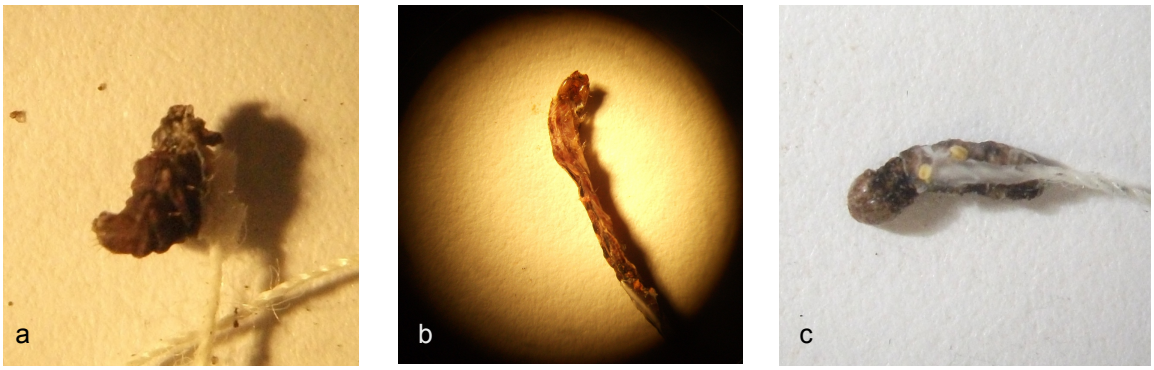

Fig. 5. Categorising the causes of death in tethered *S. nigrita*. **a)** I recognised bird attacks by a caterpillar being bitten off its line, so that a small fleshy piece remained. **b)** Caterpillars attacked by spiders were sucked dry leaving an empty skin. Often the spider was still feeding, allowing me to identify its species. **c)** Other causes of death included parasitism, infections and unidentified causes. The dead were often fed on by *Nysius groenlandicus* bugs or by mites, but these did not suck the body dry like spiders did. Apart from dying, some caterpillars simply disappeared off the line. Many of these had moulted, leaving behind a distinctive empty skin (with the forefeet intact, unlike the remnants left by birds).

After tethering I checked the caterpillars daily, removing those who had died and untangling any caterpillar whose line got caught. I split predated caterpillars into those attacked by birds and those attacked by spiders (Fig. 5).

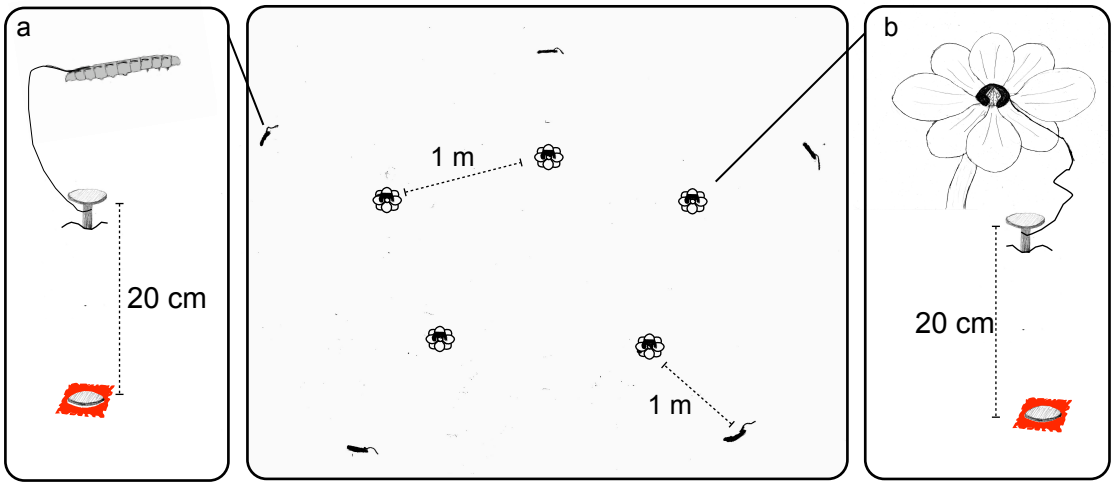

Fig. 6. The layout of bait groups, with two kinds of bait caterpillars used for detecting predation. Baits were distributed at least one metre apart on patches of avens. **a)** Tethered *S. nigrita*, in the outer ring, were tied to a nail with a ~15 cm sewing thread (or in some cases with fishing line). **b)** Dummies, in the inner ring, were tied with a ~15 cm long fishing line (0,12 mm monofilament) and balanced on an avens flower. I glued the caterpillars to their line with superglue (cyanoacrylate gel). As a marker, I nailed a small square of red crepe paper 20 cm south of each bait. When flowers wilted I moved tethered *S. nigrita* to the nearest still edible flower, and dummies I placed on the nearby ground on top of avens leaves.

2.3.2. Dummy *S. nigrita*

As my second method for measuring bird predation rates, I used dummy *S. nigrita* made of modelling clay (see e.g. Howe et al. 2009). These showed peck marks when attacked by birds (Fig. 7).

I placed 121 dummies out in the field in groups of five (Fig. 6; one group had an extra dummy). I spaced the groups out haphazardly, trying to cover as wide a range as possible (see map in Appendix 1: Fig. A1.3). In addition to these, I placed an extra 80 dummies late in the season (Fig. 4) on the few remaining patches of flowering avens. They were spaced out at one metre intervals in two large groups of 18 and 62 dummies respectively (see map in Appendix 1).

Fig. 7. Dummy *S. nigrita* used for measuring the rate of bird attacks. **a)** Dummies were 2–3 cm long, with segmentation and black felt tip spots. They were made of modelling clay (Becks Plastilin, Gomaringen, Germany). To keep them in place I glued them to a line (see Fig. 6 for details). **b)** A live *S. nigrita* for comparison, eating the stamens. I classified a dummy as bird attacked if it had moved and showed any of the following (c–e): **c)** A symmetric V-shaped cut, usually paired with a similar mark on the opposite side of the dummy. **d)** A round stab mark (presumably made by the beak tip), if paired with some other mark. **e)** A mangled dummy, squashed from both sides by a triangular object. I did not classify dummies that disappeared as being victims of bird attacks. One dummy was stepped on by a musk ox, but was easy to distinguish from a mangled (e) one.

I checked the dummies at regular intervals (daily at first, then approximately every five days after the 5th July) for bird attacks or other damage. If a dummy had fallen off its flower I lifted it back, and I replaced damaged dummies with new ones. Since birds might remember the spot where they attacked a dummy, I replaced attacked dummies at least 50 cm away, while still keeping a minimum distance of one metre to the others.

2.3.3. Dummies of other species: *C. hecla* and *G. groenlandica*

The above two methods (tethered and dummy *S. nigrita*) measured the rate of bird attacks for only one species. To check whether other species are attacked at similar rates to *S. nigrita*, I also planted dummies of *C. hecla* and *G. groenlandica* caterpillars (Fig. 8).

Fig. 8. Dummies of *C. hecla* and *G. groenlandica*. **a)** *C. hecla* made of modelling clay (Becks Plastilin), with segmentation and a black felt tip 'head'. Length 1–2 cm. The dummy in the photo has been pecked by a bird. **b)** *G. groenlandica* made of brown modelling clay, human hair and glue. Length roughly 4 cm. **c)** Empty *G. groenlandica* skin glued to a piece of modelling clay, which is perched on top of a steel nail. The skins came from parasitised caterpillars which had been mummified by *Hyposoter deichmannii*. Dummies of type a) or b) were glued to 15–20 cm of line, and tied to a nail. I marked these nails with a small square of red crepe paper.

I placed 50 *C. hecla* dummies (Fig. 8a) in two grids of 5 x 5 (one metre between dummies) by a mossy stream where I had earlier found a live caterpillar. Each dummy was next to a willow leaf (*Salix arctica*) as this appears to be the species' food plant at Zackenberg. The dummies were exposed in the field 5th – 19th August after which I checked them for bird pecks.

The *G. groenlandica* dummies were of two different types (Fig. 8b,c). I placed 20 pairs of these (i.e. one modelling clay and one skin dummy, a metre apart) next to willow leaves in a marshy area where the caterpillars are common. The pairs were at least 20 metres from each other. Since finding them proved difficult, I marked each pair with an additional ~10 cm length of red crepe nailed to the ground a metre from one of the dummies. I checked them every five days 12th July – 22nd August for bird attacks.

2.3.4. Analyses of herbivore-predator interactions

As a measure of the strength of predation, I counted daily attack rates – that is, the fraction of caterpillars attacked per day. For each type of bait (either tethered *S. nigrita* or dummy),

$$attack\,rate = \frac{a}{\sum_i d_i} \quad , \qquad (1)$$

where a is the number of attacks and d the bait days – i.e. the total number of days that the individual baits (*i)* were exposed to predation.

When calculating how long an individual bait was exposed to predators (d_i), I assumed it was exposed for the whole time period spent outdoors unless the bait died, disappeared or was attacked. In the latter cases I assumed that the bait ceased being attractive to predators (on average) halfway between when I found it gone and when I had previously checked it.

To verify that dummy *S. nigrita* gave similar results to tethered *S. nigrita*, I calculated the attack rates of both for the time period 25th June 00:00 – 11th July 00:00 (when both were present in reasonable numbers, Fig. 4).

Finally, I calculated standard errors for the attack rates using bootstrapping (see Efron & Tibshirani 1993). Briefly, I set a computer to randomly resample the individual baits (with replacement) 10^6 times, and took the standard deviation of the ensuing 10^6 attack rates. Less briefly, using the 50 *C. hecla* dummies as an example: 1) a new sample of 50 dummies was drawn randomly from the original dummies (with replacement, i.e. the same dummy could be drawn several times) 2) the attack rate was calculated for the dummies in this new sample 3) the previous two steps were repeated 10^6 times giving a distribution of 10^6 attack rates. I took the standard deviation of this (more or less normal) distribution, which corresponds to the standard error of the mean attack rate. I calculated the bootstraps using the R software (version 2.9.0).

2.4. Bringing together parasitism, predation and herbivory for *S. nigrita*

To bring together the different parts of the food web, I first estimated the parasitism of *S. nigrita* based on independently collected data, then calculated the relative strength of the measured interactions between avens, *S. nigrita*, parasitoids and predators.

For estimating parasitism, I used parasitism data of *S. nigrita* from the ongoing work on the parasitoid-lepidopteran food web (Tomas Roslin & Gergely Várkonyi, see Roslin & Várkonyi 2010). This data was gathered 17th June – 12th August 2011 by collecting lepidopteran caterpillars – both by searching the valley visually and by setting live-catching pitfall traps. A total of 437 *S. nigrita* were collected, the majority during the first weeks of the field season. These were reared in jars until they pupated or a parasite hatched, thus giving an estimate of the percentage *S. nigrita* that were parasitised when collected. I took this to be the same as the overall percentage *S. nigrita* parasitised during the whole larval period, since the parasitoids at Zackenberg mostly lay their eggs at the start of the larval period in young early instar caterpillars (Appendix 2).

To assess the relative strength of different interactions, I made them comparable by estimating their effect on fitness. For lepidopterans I calculated the fate of *S. nigrita* during their larval period – i.e. calculated how many get killed by parasitoids, birds or spiders. For the plants, I calculated the overall drop in avens fitness (measured as the weight of seed produced) due to lepidopteran herbivory.

For calculating the fate of *S. nigrita* during their larval period, I used the daily predation rates that I had measured with baits (see 2.3.) to estimate the portion predated after 25 days,

$$p_{25\,days} = 1 - (1 - p_{1\,day})^{25} \quad , \qquad (2)$$

for both bird and spider predation. Here I assumed that the rate of predation remains the same throughout the larval period for all instars, and that it takes an average of 25 days for *S. nigrita* to pupate. The latter assumption is based on observations from caterpillar rearings (T. Roslin, pers. comm.). The former is unlikely to be entirely true – spiders may,

for example, favour younger caterpillars and birds older, more visible caterpillars – but should be close enough for the accuracy required. When calculating bird predation I used the combined rate (tethered and dummy *S. nigrita*) which was measured 25th June 00:00 – 11th July 00:00 rather than the overall rate that covered the whole season, since most caterpillars had pupated by the end of this period.

To get the actual percentages of *S. nigrita* killed by parasitoids, birds and spiders, I took into account that a substantial portion of the parasitised caterpillars are predated (killing the parasitoid before it can hatch). I adjusted the parasitism by subtracting such predated caterpillars,

$$par_2 = par \times (1 - p_{25days}), \quad (3)$$

where p_{25days} is the combined bird and spider predation from Eq. 2, *par* the overall parasitism of *S. nigrita,* and *par2* the adjusted parasitism – the portion of caterpillars who actually hatch a parasitoid. This is based on the assumption that parasitised *S. nigrita* are just as likely to be predated as unparasitised ones.

To calculate the overall drop in avens fitness, I multiplied the measured fitness of each flower damage category (see 2.2.) with the portion of flowers that belonged to these categories. This gave an overall avens fitness expressed as mg seeds / flower. I compared this to the fitness of undamaged flowers.

3. Results

3.1. Plant-herbivore interactions

Examining two sets of avens flowers for damage revealed high rates of herbivory. In total, 14.4% of the flowers in ‘square plots’ showed damage caused by feeding caterpillars, and 8.3% of the flowers in ‘other plots’ (Fig. 9). This difference between the two materials

was apparently due to two exceptionally damaged square plots – without these, herbivory of the square plots was 10% and the difference was not significant ($P = 0.33$, Fisher's exact test). Bootstraps indicated herbivory rates of 10% in square plots, 8.4% in other plots, and an overall rate of 9.1% for the two materials combined (Fig. 9). All three types of flower damage (Fig. 2) were present, with damage to the pistil being most common (Fig. 9).

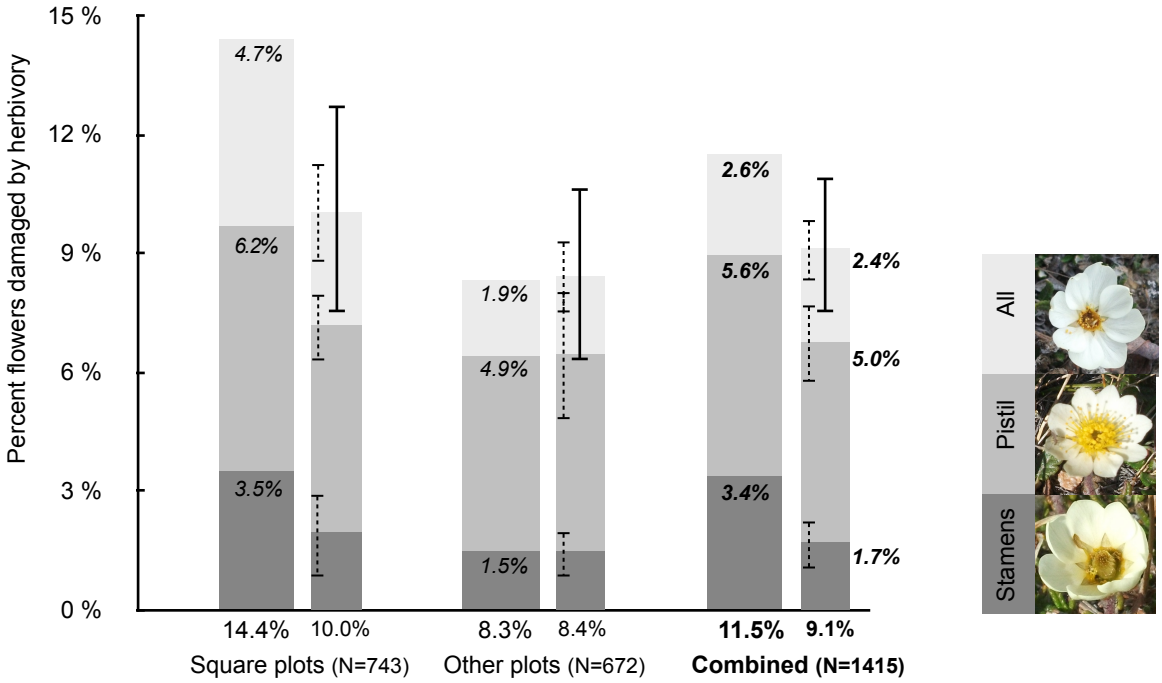

Fig. 9. Percent of avens flowers that had been eaten by caterpillars, for flowers examined in square plots, in other plots and for the two materials combined. Bars to the left show the damage actually measured in the plots, bars to the right the 'true' damage and SEM inferred by bootstrapping. The high damage in square plots (14.4% in total) was due to two outliers, with the bootstrapped value (10%) being close to that of the other plots. Overall, the results indicate that 9.1% of flowers are damaged by herbivory. Flowers showed damage to the stamens, to the pistils, or to both.

As for seed production, flowers that were eaten by caterpillars produced fewer seeds (Kruskal-Wallis $H(3) = 34.35$, $p = 1.7\text{x}10^{-7}$; Fig. 10b), and the seeds they did produce were smaller (Kruskal-Wallis $H(3) = 8.57$, $p = 0.04$; Fig. 10c). This led to their fitness, measured as the total weight of seed produced by a flower, to be lower (Kruskal-Wallis $H(3) = 39.2$, $p = 1.6\text{x}10^{-8}$; Fig. 10a). Seed production suffered the most from damage to the pistil: there was a clear progression from 'all eaten' flowers (worst seed production) via pistil and stamens to undamaged flowers (best seed production, Fig. 10).

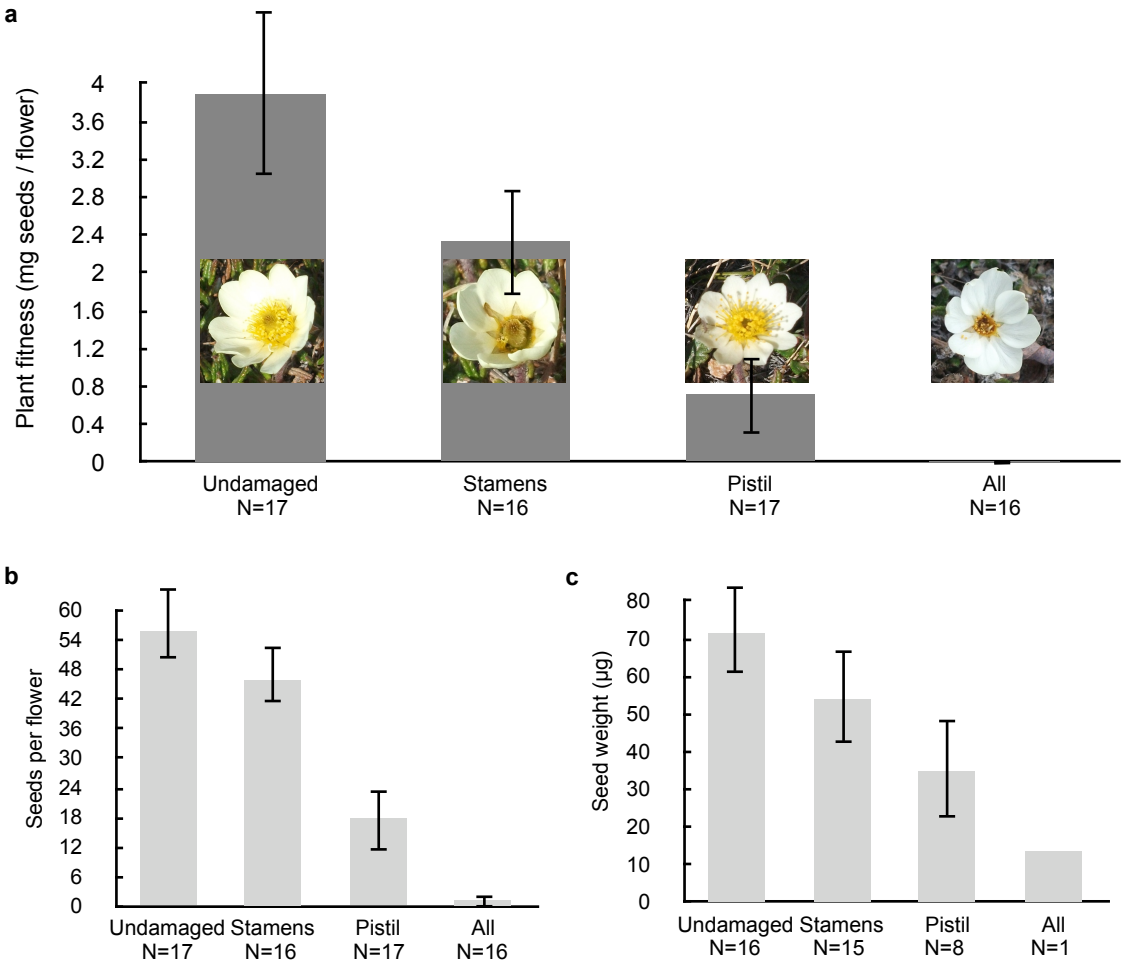

Fig. 10. Seed production of avens flowers damaged by caterpillars. Damaged flowers produced less total seed weight (**a**). This was due to their seeds being both fewer in number (**b**) and smaller (**c**). The bars show standard errors. Many of the damaged flowers produced no seeds whatsoever, hence the lower sample sizes for seed weight.

3.2. Herbivore-predator interactions

At the higher trophic level, predation of the Lepidoptera was generally low with the important exception of spider predation (Fig. 11). Tethered *S. nigrita* were exposed to predation for a total of 587.1 bait days, during which time eleven were eaten by spiders (0.019 per day) and four by birds (0.007 per day). Dummy S. nigrita were exposed for 9028 bait days and 16 were attacked by birds (0.002 per day). As for other species, dummy *C. hecla* were exposed for 678 bait days with three bird attacks (0.004 attacked per day) and *G. groenlandica* for 1652 bait days with none attacked.

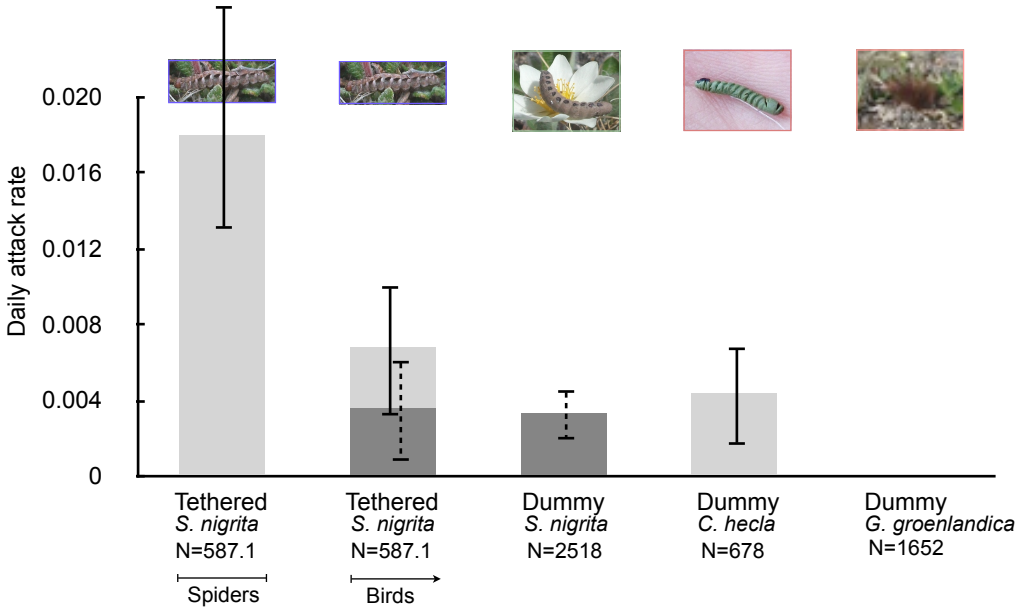

Fig. 11. Daily attack rates (portion attacked per day) for *S. nigrita*, *C. hecla* and *G. groenlandica*. Tethered *S. nigrita* were attacked by both spiders and birds, dummies by birds only. The darker bars show the attack rates during 25th June – 11th July, for verifying that dummy and tethered *S. nigrita* gave similar results. The sample sizes are expressed in bait days (see 2.3.4), and the error bars show standard errors (±1 SEM) based on bootstrapping.

During the time period used to compare dummy and tethered *S. nigrita* (25th June–11th July, Fig. 4), dummies experienced a daily attack rate by birds of 0.0033 and tethered *S. nigrita* an almost identical 0.0036 (Fig. 11). Combined, these two kinds of bait were exposed for 2398.5 bait days and were attacked 8 times (attack rate of 0.0033).

3.3. Overall parasitism, predation and herbivory for *S. nigrita*

The overall mortality of *S. nigrita* is high. During the 25 days that *S. nigrita* spend as caterpillars, an estimated 38% will be eaten by spiders and 8% by birds (based on predation rates of 0.0033 per day for birds, 0.0189 for spiders from 3.2.). As for parasitism, 15.1% of collected *S. nigrita* were parasitised, but since almost half of these (46%) get predated only 8% of *S. nigrita* actually die of a parasite (Fig. 12). Overall, 54% of *S. nigrita* die during their larval period of predation or parasitism (Fig. 12).

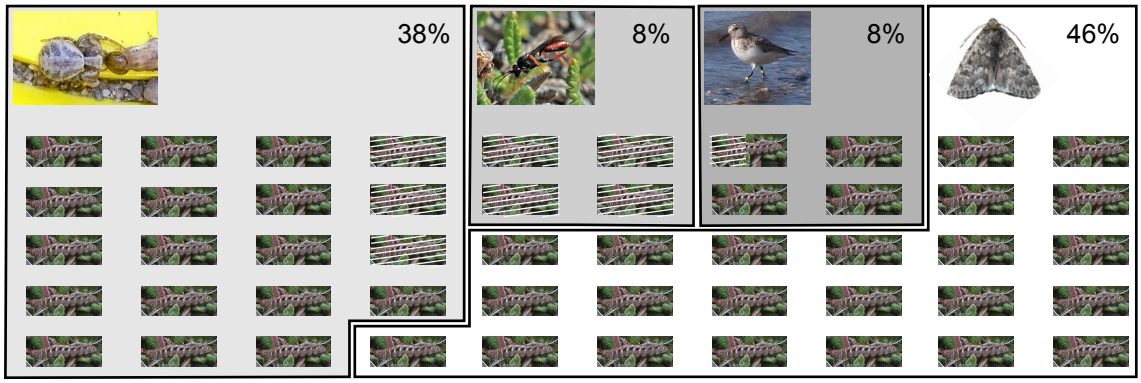

Fig. 12. The fate of an example group of 50 *S. nigrita* caterpillars over their 25 day larval period. 38% are killed by spiders, 8% by parasitoids and 8% by birds. The birds and spiders also kill parasitised caterpillars (hatched lines). Only 46% of *S. nigrita* survive predation or parasitism.

Of avens flowers, 9.1% are damaged by caterpillar feeding (3.1.). Multiplying the portion flowers in each damage category with the average fitness of the category gives an overall fitness of 3.6 mg seeds / flower, as opposed to the 3.89 mg seeds / flower of undamaged flowers. Thus the caterpillars decrease avens fitness by 7% (Fig. 13).

Fig. 13. Herbivory of an example group of 11 avens flowers and 55 units of seeds. Caterpillars cause damage to 9% of the flowers, and this decreases the overall weight of seed produced (i.e. avens fitness) by 7%.

4. Discussion

In this thesis, I measured high rates of both herbivory and predation at Zackenberg. The results reveal a tritrophic food web (plants, lepidopterans, and predators + parasites) with links which I have quantified between the trophic levels and also between predators and parasites at the highest level. Predation, especially predation by spiders, turned out to be a stronger source of mortality for Lepidoptera than parasitism. Extending the original food web beyond parasitoids and their hosts thus proved to give a much more accurate picture

of the community – indeed, the original parasitoid-lepidopteran web would have been incomplete on its own. This extended food web may in future be compared to those of lower latitudes.

4.1. Herbivory and predation at Zackenberg

Herbivory was reasonably high at Zackenberg, with 8.3%–14.4% of avens flowers showing damage caused by feeding caterpillars. Both stamens and pistil were eaten, and the damaged flowers produced fewer and smaller seeds. This herbivory has a real impact on the avens' reproduction: the overall seed production dropped by 7% from 3.9 mg per flower to 3.6 mg per flower. Moreover, this is a minimum estimate: the 'undamaged' flowers (3.9 mg seeds / flower) may have been eaten after I checked them but before I collected their seeds, and many of the smaller seeds produced by damaged flowers may well not be viable.

The herbivory was extremely variable in space: the material includes sample plots whose flowers were almost entirely eaten, untouched plots, and everything in between. This variation was evident even at scales of tens of metres. It is impossible to say if there is a similarly high variation in time, but the results do suggest that the herbivory is best envisaged as a patchwork: a rich mosaic of tiny areas with varying herbivory (cf. Gripenberg & Roslin 2007).

Predation of caterpillars turned out to be much higher than parasitism. A whole of 46% of *S. nigrita* are predated during their larval period (38% by spiders and 8% by birds), versus 15% that are parasitised and 8% that die of parasitism. While the methods used may have distorted these rates somewhat (e.g. tethering of live caterpillars could make them more vulnerable to spiders, see Weseloh 1990 as cited in Jervis 2005:450), the overall scales are clear. At Zackenberg, spider predation is more than twice as great as parasitism and bird predation is half of parasitism. Rates of bird predation for *C. hecla* were similar (although with low sample size), whereas the *G. groenlandica* were not predated (possibly due to

the experiment having started too late, when the *G. groenlandica* were largely in hibernation).

Bird predation was unexpectedly low, 8% over a 25-day period (0.3% per day). This is much less than what has been commonly reported from elsewhere (daily rates for Lepidoptera from natural areas: 1.8% in Finland, Mäntylä et al. 2008; 4%–10% in Estonia, Remmel & Tammaru 2009; 0–4% in Chile, Lluch et al. 2009; 11.6% in the Phillippines, Posa et al. 2007). It is tempting to speculate that the difference could be caused by differences in latitude: Greenlandic abiotic conditions are harsh, most birds are migratory, and thus the bird densities (approx. 25 territories / km^2, see Table 1) are likely lower than in warmer climates. However, publication bias for high predation rates cannot be ruled out, as it is quite conceivable that low predation rates are rarely detected in short studies or are not deemed worth publishing (for a review of publication bias see e.g. Møller & Jennions 2001).

4.2. Indirect interactions at Zackenberg

In recent years the concept of apparent competition, where species compete by sharing a predator rather than a resource, has received increasing attention (e.g. Holt & Lawton 1994, Van Nouhuys & Hanski 2000, Van Veen et al. 2006, Van Veen et al. 2008). The Zackenberg lepidopteran community could well be worth studying in this context, since the results of this thesis show they are not resource-limited (i.e. there is little competition for resources) but are predated by birds, spiders and parasitoids. In such a predator-rich system, there is a strong potential for apparent competition, apparent mutualism (see Tack et al. 2011), or more complex forms of predator-mediated indirect interactions between species (Holt & Lawton 1994).

In this context, it is worth noting that the predators and parasitoids at Zackenberg interact directly as well as indirectly: whenever predators eat a parasitised caterpillar, they also kill the parasitoids it contains. Thus a substantial portion of parasitoid larvae are predated at Zackenberg, with the exact figure depending on whether parasitised and unparasitised

caterpillars are equally likely to be predated. Whether this is so is an open question: there are indications that birds prefer unparasitised caterpillars (Fritz 1982) and that ants favor more vulnerable parasitised caterpillars (Jones 1987), but overall the relative vulnerability of parasitised caterpillars varies between studies with no general rule discernible (Fritz 1982). However, the Zackenberg predators likely make little distinction between parasitised and unparasitised *S. nigrita* since parasitism is roughly the same for all instars (Appendix 2; a significant preference for e.g. parasitised caterpillars would cause lower parasitism in older instars). Under this assumption, a whole of 46% of parasitoid larvae are predated by birds and spiders– with obvious implications for parasitoid population size, and less obvious ones when it comes to the direct and indirect interactions in this system.

To see how the above could affect direct and indirect interactions between populations, consider two example hypotheses on the nature of interactions at Zackenberg:
1) Apparent competition between lepidopteran species may be weaker than expected.
Reason: Naively, one would expect that an increase in lepidopteran population would cause both increased predation and parasitism. This in turn may increase mortality of other lepidopterans (i.e. cause apparent competition). *But* when predation increases, part of the increase will be inflicted on parasitised caterpillars (which would have died anyway) and the mortality of parasitoid larvae will also increase. Parasitism, measured as the percent lepidopteran mortality caused by parasitoids, will thus increase less than naively expected – indeed, it is quite conceivable that the increased predation could lead to a *decreased* parasitism.
2) Competition between parasitoids and predators is biased in favor of predators.
Reason: When predators increase in number, they decrease lepidopteran populations and thus compete with parasitoids for food. But they also eat more parasitised caterpillars, increasing parasitoid mortality. So parasitoids are at a disadvantage through being both competitors and prey, whereas predators need only cope with competition. A similarly one-sided interaction may potentially exist between the two predator guilds: I did not measure the predation of spiders by birds, but it seems likely that such predation occurs.

It is not difficult to generate further hypotheses such as these – all variants of the general question 'If a population changes, how are the other populations affected?' with the interaction between parasitoids and predators taken into account. Nor are the hypotheses necessarily restricted to the Zackenberg community alone, but may have general relevance in any host-parasite community where predation is significant. In general, parasitoids could alleviate the effects of apparent competition, apparent mutualism and other indirect interactions (e.g. as in hypothesis 1 above).

As a final note, generating and testing such hypotheses only becomes possible with a detailed knowledge of the community. In the Zackenberg community, for example, the links between populations have been quantified – identifying the pathways through which populations may interact. But it is not known how these quantified links respond to changes in population densities (e.g. how much predation increases when a lepidopteran population does so). In other words, the quantitative web described in this thesis allows one to infer that apparent competition is likely to occur, but does not tell exactly how strong that apparent competition is.

4.3. The effect of biotic and abiotic factors

A food web is valuable in itself, as a description of a community's structure. Ecology at its most interesting, however, involves not only description but also prediction – the drawing of general inferences on how a community behaves. In this context, some inferences may be made on the Zackenberg community and how it is structured by biotic and abiotic factors. Also, since Zackenberg is a high latitude area (i.e. low productivity and harsh climate), a future comparison with other food webs would shed light on some of the most fundamental questions in ecology – indicating how communities in general are structured by biotic and abiotic factors.

4.3.1. How do biotic and abiotic factors regulate the Zackenberg community?

The measured levels of predation and herbivory fit the traditional conception of a tritrophic food web where plants are limited by their resources, herbivores by predators and the predators by their food supply (Hairston et al. 1960, Fretwell 1977). (Though the existence of three distinct trophic levels is perhaps questionable since parasitoids are predated). As far as the Lepidoptera and their food plants are concerned the world *is* green (Fretwell 1977), or rather a flowery white-yellow; with 91% of avens flowers entirely untouched by caterpillars, lack of food (bottom-up) does not seem to restrict lepidopteran population sizes. Nor are plant densities likely to be limited by top-down lepidopteran herbivory when that herbivory only drops fitness by 7% (other herbivory by e.g. musk ox could, however, have a stronger top-down effect). As for herbivores being regulated by predation, predators and parasitoids appear to have a strong impact on the lepidopterans, killing 46% of caterpillars.

On the abiotic side, Northeast Greenland is an area of harsh climatic conditions – if abiotic factors show in food web structure anywhere, they should do so here. However, only somewhat tentative inferences are possible based on the (biotic) food web alone: Based on the results, the climate could be a significant regulator of lepidopteran populations; spiders and birds kill 46% of caterpillars, leaving almost 54% to die of other causes (‘almost’, since some must survive and breed). These other causes could include (biotic) disease and (abiotic) exposure during the winter hibernation. The high spider predation coupled with low bird predation is consistent with the idea of endotherm predators being at a disadvantage in arctic conditions (an assumption of the EE-hypothesis; Oksanen & Oksanen 2000). Also, the Zackenberg food web has several trophic levels and complex interactions between species, which does not fit conventional extrapolations on the structure of high latitude, low productivity ecosystems (e.g. Pimm 1982, Kitching 2000, Van der Wal & Hessen 2009).

It has been tentatively suggested that the relative strength of predation and parasitism varies with latitude, although whether this is be caused by differences in climate, primary productivity or species richness remains unexplained: based on life tables from temperate

and tropical areas, parasitism should become stronger and predation weaker at high latitudes (Hawkins et al. 1997). This is not supported by my results from Zackenberg where spider predation is the dominant cause of death for *S. nigrita*, far outstripping parasitism – although the low bird predation does fit this pattern.

4.3.2. Comparing food webs that stem from varying biotic and abiotic conditions

Looking at the Zackenberg food web alone, it is possible to infer something of the nature of its biotic interactions (e.g. the discussion above), but inferences on abiotic factors are already more speculative. Yet a knowledge of how biotic and abiotic factors affect the community would be of value – not only due to the general ecological interest, but also because the area will likely experience both biotic and abiotic changes. Ecology at its best is a predictive science, and it should be possible to predict what happens when biotic conditions change (e.g. ants spread to the area) or abiotic conditions change (e.g. the climate warms).

The obvious solution to this would be to compare several food webs, from areas with different abiotic conditions (i.e. from different latitudes). Similar comparisons of food webs have been successfully used to gauge human impact on tropical ecosystems, by comparing the structure of webs from human-impacted and natural areas (e.g. Tyliakis et al. 2007, Valladares et al. 2012). In such a comparison the Zackenberg food web (once the parasitoid-host interactions have been described) would be a valuable data point, as it describes a High Arctic ecosystem with low productivity and harsh climate.

However, any comparison of food webs requires webs that are comparable. That is, the webs should be more or less complete, omitting no relevant interactions in the community. When it comes to Zackenberg, my results indicate that a mere parasitoid-host web is insufficient in this sense: since predation is comparable to parasitism (or actually much stronger than parasitism), an ecologically relevant web must include at least the lepidopterans, their parasites and predators. Thus in the context of comparing food webs from different areas – whether for latitudinal comparisons as proposed here or for gauging

human impact (as in Tyliakis et al. 2007, Valladares et al. 2012) – the possibility of parasitoid-host webs being incomplete may be worth bearing in mind. Especially since the overwhelming majority of quantitative food webs described to date are parasitoid-host webs (e.g. Memmot et al. 1994, Müller et al. 1999, Rott & Godfray 2000, Valladares et al. 2001, Lewis et al. 2002, Tyliakis et al. 2007) with only some webs taking predation into account (e.g. Tscharntke 1992, and to some extent Brown et al. 1995, Pocock et al. 2012).

4.4. Conclusions

The results of this study of a High Arctic area reveal an extensive tritrophic food web, where lepidopterans eat substantial amounts of their food plants, are preyed on by spiders, parasitoids and birds (in that order), and the parasitoids are also preyed on by their competitors. This food web would tentatively appear to be more complex and have higher rates of predation than expected for such a high latitude, low productivity ecosystem. In particular, the intricate interaction between predators and parasitoids may have consequences for apparent competition and other indirect interactions in the community. Adding quantitative data on predation and herbivory proved worthwhile; a parasitoid-lepidopteran web on its own would not have captured the complexity of this system.

5. Acknowledgements

As is the case with all theses, the list of people who deserve thanks for contributions, advice and support is both considerable and incomplete. I would like to extend my gratitude to:

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- Finally if somewhat unconventionally: the numerous living creatures – lepidopteran, avian, parasitoid or otherwise – who it was my pleasure to observe and interact with during the summer 2011.

6. References

Agrawal A.A. 1998: Induced responses to herbivory and increased plant performance — *Science* 279: 1201–1202.

Banašek-Richter C., Bersier L.-F., Cattin M.F., Baltensperger R., Gabriel J.-P., Merz Y., Ulanowicz R.E., Tavares A.F., Williams D.D., de Ruiter P.C., Winemiller K.O. & Naisbit R.E. 2009: Complexity in quantitative food webs — *Ecology* 90: 1470–1477.

Bay C. 1998: *Vegetation mapping of Zackenberg valley, Northeast Greenland.* — Danish Polar Center & Botanical Museum, University of Copenhagen. 29 pp.

Brown J. M., Abrahamson W. G., Packer R. A. & Way P. A. 1995: The role of natural-enemy escape in a gallmaker host-plant shift — *Oecologia* 104: 52–60.

Denno R.F., McClure M.S. & Ott J.R. 1995: Interspecific interactions in phytophagous insects: Competition reexamined and resurrected — *Annual Review of Entomology* 40: 297–331.

Efron B. & Tibshirani T.J. 1993: *An introduction to the bootstrap* — Chapman and Hall. London. 436 pp.

Egerton F.N. 2007: Understanding Food Chains and Food Webs, 1700–1970 — *Bulletin of the Ecological Society of America* 88: 50–69.

Fretwell S. D. 1977: The regulation of plant communities by food chains exploiting them — *Perspectives in Biology and Medicine* 20: 169–185.

Fritz R.S. 1982: Selection for host modification by insect parasitoids — *Evolution* 36: 283–288.

Goldwasser L. & Roughgarden J. 1997: Sampling Effects and the Estimation of Food-Web Properties — *Ecology* 78: 41–54.

Gripenberg S. & Roslin T. 2007: Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology — *Oikos* 116: 181–188.

Hairston N.G., Smith F.E. & Slobodkin L.B. 1960: Community structure, population control, and competition — *The American Naturalist* 94: 421–425.

Hawkins B.A., Cornell H.V. & Hochberg M.E. 1997: Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations — *Ecology* 78: 2145–2152.

Holt R.D. & Lawton J.H. 1994: The ecological consequences of shared natural enemies — *Annual review of Ecology and Systematics* 25: 495–520.

Howe A., Lövei G.L. & Nachman G. 2009: Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem — *Entomologia Experimentalis et Applicata* 131: 325–329.

Hunter M.D. & Price P.W. 1992: Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities — *Ecology* 73: 724–732.

Jervis M.A. 2005: *Insects as natural enemies: a practical perspective* — Springer, Dortrecht, The Netherlands. 748 pp.

Jones R.E. 1987: Ants, parasitoids, and the cabbage butterfly Pieris rapae — *Journal of Animal Ecology* 56: 739–749.

Kaplan I. & Denno R.F. 2007: Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory — *Ecology Letters* 10: 977–994.

Kitching R.L. 2000: *Food webs and container habitats: The natural history and ecology of phytotelmata* — Cambridge University Press, Cambridge. 431 pp.

Lewis O.T., Memmott J., Lasalle J., Lyal C.H.C., Whitefoord C. & Godfray H.C.J. 2002: Structure of a diverse tropical forest insect-parasitoid community — *Journal of Animal Ecology* 71: 855–873.

Lluch A., González-Gómez P. L., de la Vega X. & Simonetti J. A. 2009: Increased avian insectivory in a fragmented temperated forest — *Community Ecology* 10: 206–208.

Martinez N.D., Hawkins B.A., Dawah H.A. & Feifarek B.P. 1999: Effects of sampling effort on characterization of food–web structure — *Ecology* 80: 1044–1055.

Meltofte H., Christensen T.R., Elberling B., Forchhammer M.C. & Rasch M. 2008: Introduction – In: Meltofte H., Christensen T.R., Elberling B., Forchhammer M.C. & Rasch M. (eds.), *Advances in Ecological Research* 40: 1–12. 563 pp.

Memmott J., Godfray H.C.J. & Gauld I.D. 1994: The structure of a tropical host-parasitoid community — *Journal of Animal Ecology* 63: 521–540.

Møller A.P. & Jennions M.D. 2001: Testing and adjusting for publication bias — *Trends in Ecology & Evolution* 16: 580–586.

Morewood W.D. & Ring R.A. 1998: Revision of the life history of the High Arctic moth Gynaephora groenlandica (Wocke) (Lepidoptera: Lymantriidae) — *Canadian Journal of Zoology* 76: 1371–1381.

Murdoch W.W. 1966: "Community structure, population control, and competition"–A critique — *The American Naturalist* 100: 219–226.

Müller C.B., Adriaanse I.C.T., Belshaw R. & Godfray H.C.J. 1999: The structure of an aphid–parasitoid community — *Journal of Animal Ecology* 68: 346–370.

Mäntylä E., Alessio G.A., Blande J.D., Heijari J., Holopainen J.K., Laaksonen T., Piirtola P. & Klemola T. 2008: From plants to birds: higher avian predation rates in trees responding to insect herbivory. *PLoS ONE* 3: e2832. doi:10.1371/journal.pone.0002832

Oksanen L. & Oksanen T. 2000: The logic and realism of the hypothesis of exploitation ecosystems — *The American Naturalist* 155: 703–723.

Pocock M.J.O., Evans D.M & Memmott J. 2012: The robustness and restoration of a network of ecological networks — *Science* 335: 973–977.

Posa M.R.C., Sodhi N.S. & Koh L.P. 2007: Predation on artificial nests and caterpillar models across a disturbance gradient in Subic Bay, Philippines — *Journal of Tropical Ecology* 23: 27–33.

Power M.E. 1992: Top-down and bottom-up forces in food webs: do plants have primacy? — *Ecology* 73: 733–746.

Pimm S.L. 2002: The length of food chains — In: Pimm S.L. (ed.), *Food webs*: 99–130. The University of Chicago Press, Chicago. 219 pp.

R Development Core Team 2009: *R: A language and environment for statistical computing* — R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available: http://www.R-project.org.

Remmel T. & Tammaru T. 2009: Size-dependent predation risk in tree-feeding insects with different colouration strategies: a field experiment — *Journal of Animal Ecology* 78: 973–980.

Roslin T. & Várkonyi G. 2010: A high Arctic food web — In: Jensen, L.M. & Rasch M. (eds.), *Zackenberg Ecological Research Operations, 15th Annual Report 2009*: 108–111. National Environmental Research Institute, Aarhus University. 134 pp.

Rott A.S. & Godfray H.C.J. 2000: The structure of a leafminer–parasitoid community — *Journal of Animal Ecology* 69: 274–289.

Tack A.J.M., Gripenberg S. & Roslin T. 2011: Can we predict indirect interactions from quantitative food webs? – an experimental approach — *Journal of Animal Ecology* 80: 108–118.

Tscharntke T. 1992: Cascade effects among four trophic levels: bird predation on galls affects density–dependent parasitism — *Ecology* 73: 1689–1698.

Tyliakis J.M., Tscharntke T. & Lewis O.T. 2007: Habitat modification alters the structure of tropical host–parasitoid food webs — *Nature* 445: 202–205.

Valladares G., Cagnolo L. & Salvo A. 2012: Forest fragmentation leads to food web contraction — *Oikos* 121: 299–305.

Valladares G.R., Salvo A. & Godfray H.C.J. 2001: Quantitative food webs of dipteran leafminers and their parasitoids in Argentina — *Ecological Research* 16: 925–939.

Van der Waal R. & Hessen D.O. 2009: Analogous aquatic and terrestrial food webs in the high Arctic: The structuring force of a harsh climate — *Perspectives in Plant Ecology, Evolution and Systematics* 11: 231–240.

Van Nouhuys S. & Hanski I. 2000: Apparent competition between parasitoids mediated by a shared hyperparasitoid — *Ecology Letters* 3: 82–84.

Van Veen F.J.F., Morris R.J. & Godfray H.C.J. 2006: Apparent competition, quantitative food webs, and the structure of phytophagous insect communities — *Annual Review of Entomology* 51: 187–208.

Van Veen F.J.F., Müller C.B., Pell J.K. & Godfray H.C.J. 2008: Food web structure of three guilds of natural enemies: predators, parasitoids and pathogens of aphids — *Journal of Animal Ecology* 77: 191–200.

White T.C.R. 1978: The Importance of a relative shortage of food in animal ecology — *Oecologia* 33: 71–86.

Appendix 1: Maps of the research area

I carried out this research in Northeast Greenland in the Zackenberg valley, mainly near the river mouth (Fig. A1.1). The bird densities were measured from a 7.77 km^2 area on the east bank of the river (Fig. A1.2). The main study area contained bait *S. nigrita* for measuring predation, and avens plots for measuring herbivory (Fig. A1.3).

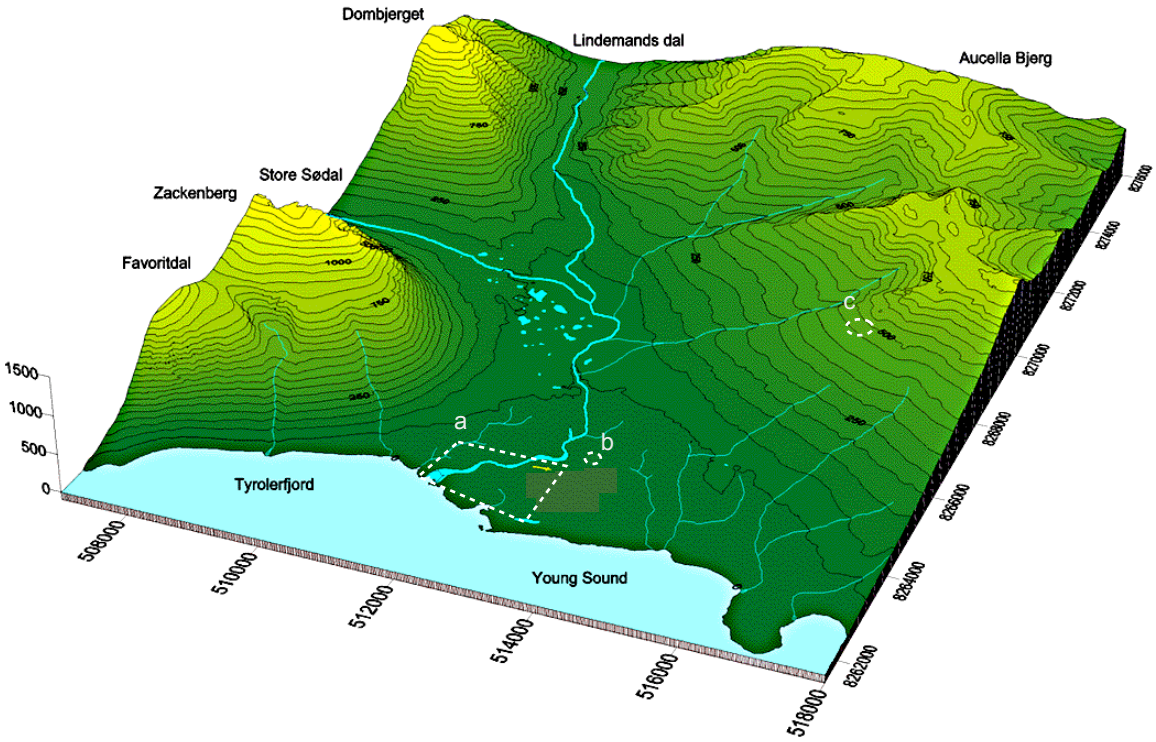

Fig. A1.1. Overview map of Zackenberg valley (modified from http://www.zackenberg.dk/). Distances are in metres in the UTM coordinate system (27X). **a)** The main study area, containing 24 groups of bait *S. nigrita* and 22+65 avens flower plots. These are shown in greater detail on the next page. **b)** 40 dummy *G. groenlandica* (see 2.3.3.) **c)** 50 dummy *C. hecla* (see 2.3.3.)

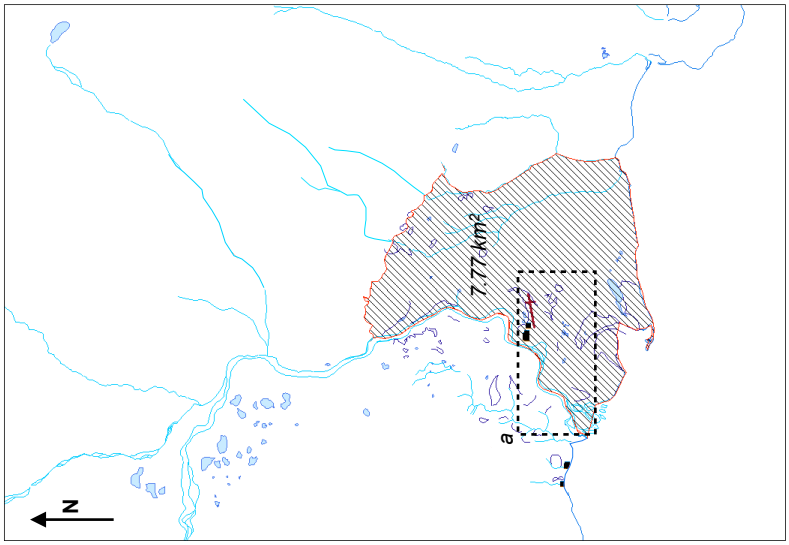

Fig. A1.2. Area used to estimate bird densities at Zackenberg. The shaded 7.77 km^2 area (50 m below sea level) contained a total of 188–207 bird territories (Table 1). The dashed line (**a**) shows the main study area. Map courtesy of Jannik Hansen.

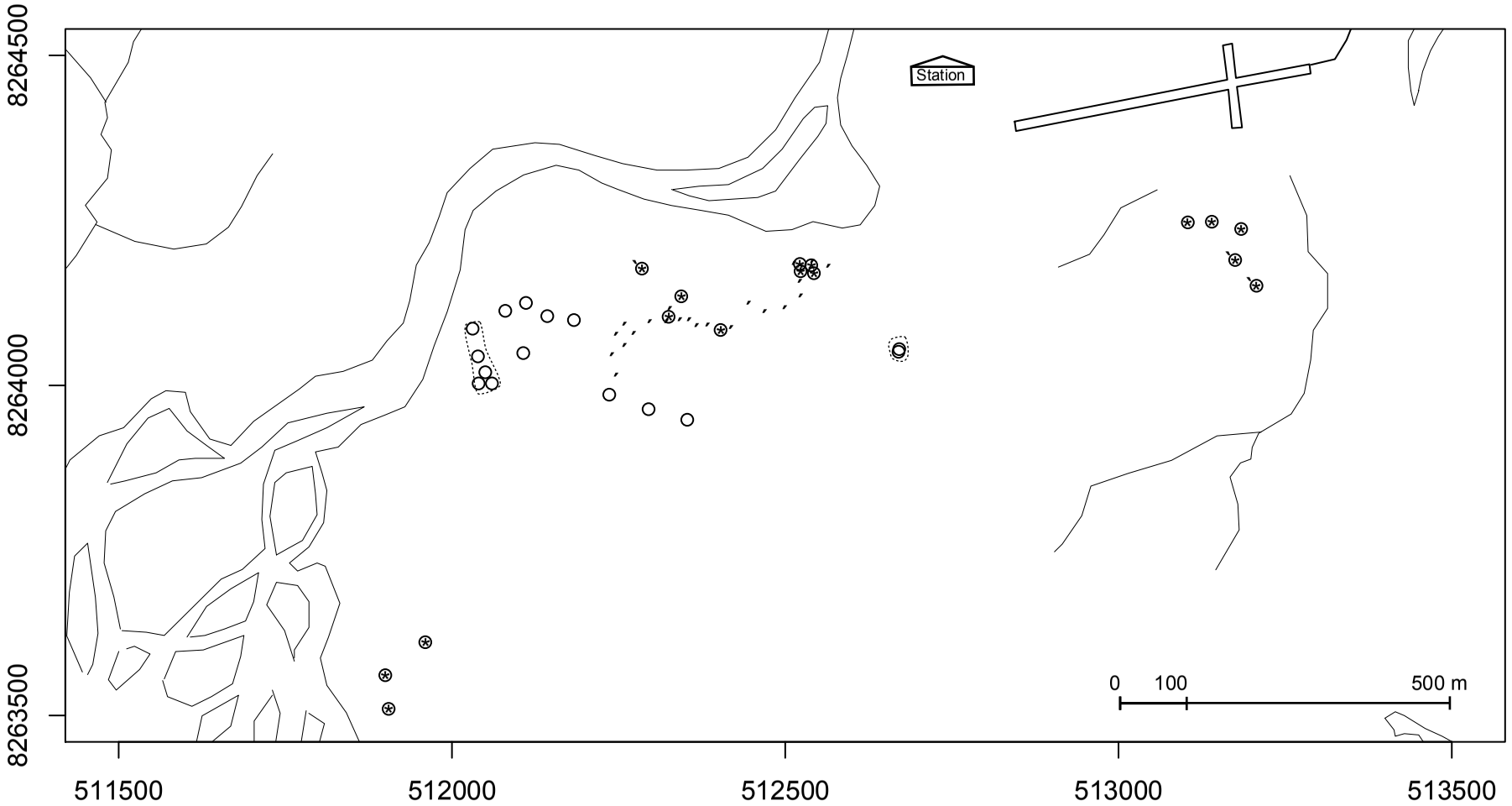

Fig. A1.3. Map of *S. nigrita* bait used for detecting predation (see 2.3.) and of sampling plots used for measuring herbivory of avens flowers (see 2.2.). These were in an area bounded by the river, Zackenberg research station and the landing strip. Distances are in the UTM coordinate system (27X).

- ○ Group of five dummy *S. nigrita.* Two compound groups placed in autumn (⬚) contained 18 + 62 dummies. (bird predation)
- ⊛ Group of five dummy and five tethered *S. nigrita.* (bird and spider predation)
- ⬞ Square plot. (percent flowers damaged and seed production of damaged flowers)

'Other plots' were next to 13 of the 16 "⊛" groups; the three groups without other plots next to them are marked ⊛. (percent flowers damaged)

Appendix 2: Early instar parasitism of *S. nigrita*

In my calculations on parasitism (section 2.4.) I assumed that caterpillars are parasitised when young (e.g. as first instars or eggs), rather than throughout the larval period. This assumption plays a vital role in determining the true strength of parasitism from the observed parasitism of collected caterpillars: only if caterpillars are no longer vulnerable to parasitism when collected is the parasitism observed in them equal to the overall parasitism during the whole larval period.

There are two arguments for early parasitism of *S. nigrita* at Zackenberg: 1) The percentage parasitism was the same for all collected sizes of caterpillar (Fig. A2.1). Had they been parasitised throughout the larval period, older instars would have been more parasitised due to having been exposed longer. 2) Of the hatched parasitoids that have been identified – *Hyposoter frigidus, Microplitis lugubris, Diadegma majale and Mesochorus sp. cf. agilis* – all but one are species that parasitise young caterpillars (the last is a hyperparasitoid; Gergely Várkonyi pers. comm.)

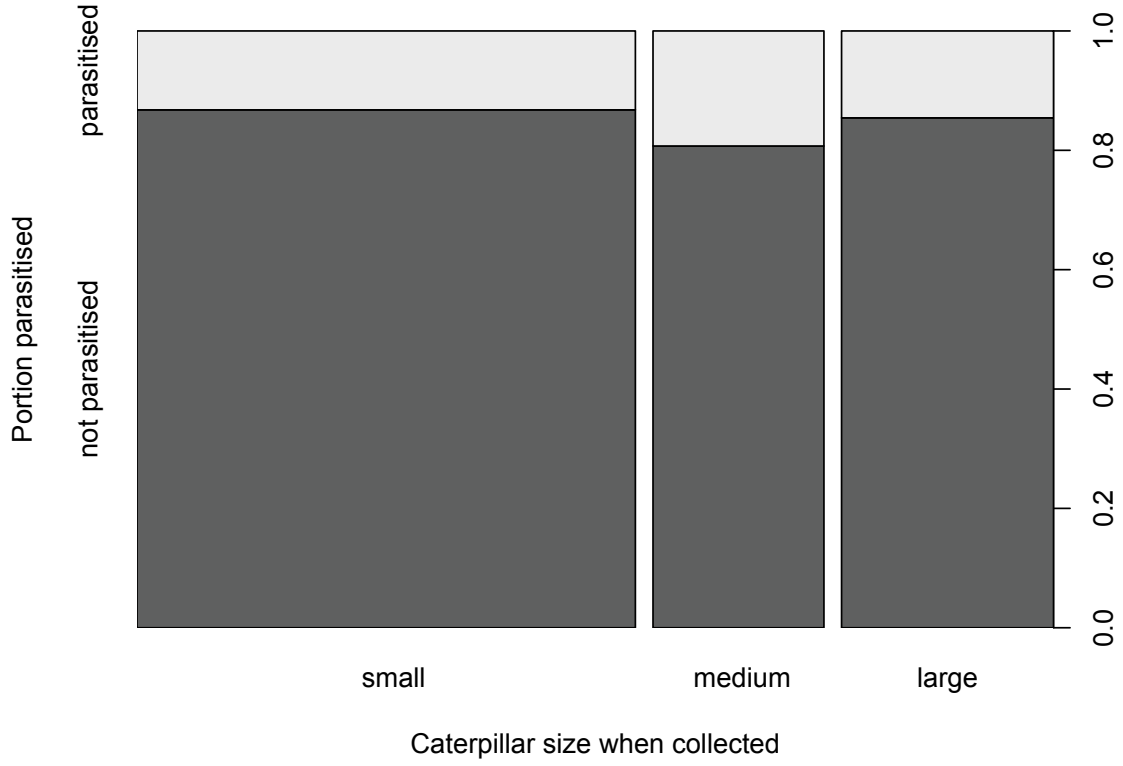

Fig. A2.1. Parasitism of different instars of collected *S. nigrita* caterpillars in 2011. I classified first and second instars as small, third instars as medium and anything above as large. The same portion are parasitised irrespective of size ($X^2(2)=1.81$, $p=0.41$), indicating that parasitism occurs early in the larval period in eggs or first instar caterpillars.